

The University of Chicago

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CORTICAL PROJECTIONS IN ESCAPE
AND AVOIDANCE CONDITIONING
IN DOGS

A DISSERTATION SUBMITTED TO THE FACULTY OF THE
DIVISION OF BIOLOGICAL SCIENCES IN CANDIDACY
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF PHYSIOLOGY

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In the study of the neurophysiology of conditioning, the surgical approach has been employed quite extensively. In most of the extirpation experiments reported, the investigators determined whether an animal can or cannot acquire a particular conditioned response after the extirpation. In some reports, however, the animals were previously trained and the retention of the acquired performance tested after the extirpation. It is the latter approach that has been adopted in this study for comparing the effects of various cortical extirpations on two different types of conditioning—escape and avoidance.

The escape type of conditioning (Hilgard and Marquis, 1940, p. 56) has been little studied either from a descriptive or from an analytic point of view. It deserves more attention than it has received because, as Guthrie has pointed out, it may play an important rôle in many types of human learning (Guthrie, 1938, p. 89–105). The avoidance type of conditioning, on the other hand, has received considerable attention but not from the standpoint of the neural pathways involved in the normal intact animal.

It might be well to make clear the similarities and differences of classical, avoidance, reward, and escape conditioning. To simplify the discussion, the conditioned stimulus, unconditioned stimulus, conditioned response, and unconditioned response will be indicated respectively by c-s, u-s, c-r, u-r.

In classical conditioning a u-s elicits the desired response, and the c-s is followed by the u-s on every trial, even if the animal responds correctly to the c-s. When the u-s is a noxious one, the training is sometimes referred to as non-avoidance conditioning. For example, in leg-flexion conditioning, in which a sound is the c-s and electrical stimulation of a paw the u-s, the electrical stimulus is made to follow the sound on each trial by means of electrodes attached to the paw. It is given (as the so-called reinforcement) even if the animal lifts its paw to the c-s.

In avoidance conditioning the u-s must be a noxious one, and it is introduced after the c-s on every trial only during the initial stages of training. When the animal does respond correctly to the c-s, it avoids the noxious u-s. One way of conducting avoidance conditioning is to supply electrical stimulation of one paw by means of a grill upon which the paw rests, so that if the dog lifts its paw to the c-s it will not receive the electrical stimulus.

In reward conditioning, the desired response is performed in the presence of the c-s by trial and error, and the correct performance is followed immediately by a bit of food. There is no u-s. After a number of trials, the animal performs the correct response immediately upon application of the c-s. An example of this is an experiment in which a guinea pig was conditioned to turn its head to one side

in response to the sound of a buzzer (Grindly, 1932). The animal was placed in a box, the buzzer turned on, and when the animal accidentally turned its head to the right side, a carrot was immediately presented by means of a lever, and the buzzer turned off. After a number of trials, the guinea pig would turn its head to the right immediately to the sound of the buzzer.

In escape conditioning, the c-s must be an annoying one which induces random activity, and there is as above no u-s. The c-r is hit upon by accident and serves to remove the annoyance. After a number of trials, the animal performs the correct response immediately upon application of the c-s. The only examples of this kind of conditioning reported consist of a few experiments performed on rats as subjects (Mowrer, 1940; Muenzinger and Fletcher, 1936) in which the animals could escape from an electrical stimulus applied through a grill on the floor of a cage by running to a certain designated place.

Thus, in classical and avoidance conditioning there is a u-s which is used to elicit the desired response, whereas in reward and escape conditioning there is no u-s. Further, in classical and avoidance conditioning the reinforcement is identical with the u-s, whereas in reward and escape conditioning the reinforcement is something which in itself does not elicit the desired response. In classical conditioning the reinforcement is applied on every trial, whereas in avoidance conditioning the reinforcement is given only on those trials in which the animal fails to respond to the c-s. In reward conditioning the reinforcement is positive (a bit of food), whereas in escape conditioning the reinforcement is negative (the escape from an annoyance). In other words, in classical and avoidance conditioning the previously indifferent stimulus (c-s) replaces the originally effective stimulus (u-s), involving the principle of substitution. In reward and escape conditioning, where there is no u-s, the principle of substitution (in its usual sense) cannot be invoked.

Two major drawbacks in the procedures so far reported for studying escape conditioning are that the c-s is applied to widely separated parts of the body simultaneously (all four paws) and that the correct response includes all four legs (a running response). Many different parts of the central nervous system are therefore involved. This extensivity of activity makes it difficult to use extirpation methods for localizing particular pathways that may be involved. In this study (1) a method was developed for escape conditioning, in which the c-s was applied to a spot on the body surface and the correct response consisted of the discrete flexion of a single leg, thus making possible extirpation of particular portions of sensory and motor projection pathways, (2) the effects of hemidecortication on previously conditioned escape and avoidance responses were compared, and (3) on the basis of the experimental results, hypotheses were formulated as to the neural mechanisms involved in the two types of conditioning.

CONDITIONING A DISCRETE ESCAPE RESPONSE: PROCEDURE AND RESULTS. An ordinary conditioning harness was used to restrain the dog's movements, and a tetanizing current, applied to a particular spot on the body surface, was the c-s. The stimulating electrode was 1.1 cm. in diameter, the indifferent electrode 5.0. The dog was first accustomed to a current by increasing the strength gradually

(accompanied by petting of the animal) until an intensity which produced a visible twitching at the site of stimulation could easily be tolerated. This twitching was used as a measure of the strength of the stimulus and permitted maintenance of the stimulus-strength at constant value when this was desired. A physical measure of the stimulus strength (such as the inductorium setting) was found to be unsatisfactory because it did not indicate the degree of stimulation of the receptor organs involved. The dog was then placed in a room by itself and observed through a window from an adjoining room, the animal being unable to see the observer. The tetanizing current was gradually increased in intensity until a value was found which produced restlessness on the part of the dog within a period of forty seconds. The most prominent feature of the restlessness was usually a stepping motion involving all four legs. That the current produced only a tingling sensation and was not painful was ascertained by testing it on human subjects.

The forepaws rested upon pedals so wired that the lifting of one certain forepaw would irreversibly turn off the tetanizing current, the current thus remaining off even after the foot was replaced on the pedal. The paw had to be lifted about two inches before the response was effective. Thus in its restlessness, the dog would accidentally lift the paw that turns off the current. This response will be referred to as the correct response.

The time interval between the starting of the current and the lifting of the correct paw was used as a measure of learning. This was represented as the median of the response time values per session. An electric clock, which was started by the tetanizing current switch and was stopped by the lifting of the correct pedal, permitted a measurement of the time interval to the nearest one-tenth second. An additional measure of learning was the percentage of correct first movements per session.

The time interval between successive trials was varied irregularly over a range of ten seconds to five minutes, with most of the intervals being less than one minute. Forty trials or one hour, whichever came first, was the duration of each session. Sessions were run once per day and five times per week.

Three types of experiment were conducted. In the first type, carried out on seven dogs, a tetanizing current was applied to the left side of the body in the lumbar region and the correct response was a lifting of the right forepaw. All seven dogs were found to be capable of learning the response. The composite performance curve for these dogs is shown in figure 1A.

The mean number of sessions required to learn the response was 2.3. After learning was complete, the medians of the response times per session showed a mean value of 1.0 second. Both of these means were statistically highly significant the *p* value of Fisher (1938) being less than 0.001.

In the second type of experiment, carried out on four dogs, the attempt was made to teach them to discriminate between two spots on the body surface. A tetanizing current applied to the left side of the body in the lumbar region was turned off by lifting of the right forepaw, whereas a current applied to the left side of the thorax was turned off by a lifting of the left forepaw. The two spots

on the body surface were used in random succession from the start of the experiment. In these experiments, the measures of learning were the median response time per session and the percentage of correct responses (or correct first movements) per session. Three of the four dogs were able to learn the discrimination, and their composite performance curves are shown in figure 1C.

An analysis of the data for these animals, using in part the statistical methods described by Fisher (1938), reveals the following information. Each of the mean values cited is statistically highly significant, p being less than 0.001 in all cases

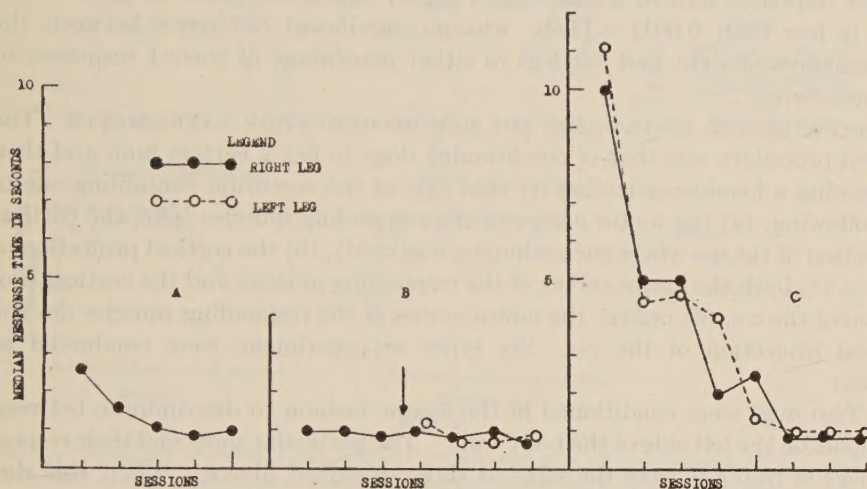


Fig. 1. Composite performance curves showing the decrease in response time with successive sessions of escape conditioning of leg-flexion in dogs. A. No discrimination involved, one spot only being used. Each point represents the mean value from seven dogs. B. Discrimination between two spots on the body surface, the response to one of the spots being learned first and then the other spot introduced in random order with the first one. The two spots were paired with different responding legs. Only the last portion of the single-spot curve is shown, and the second spot was introduced at the arrow. Each point represents the mean value from three dogs. C. Discrimination between two spots on the body surface, the two spots being used in random order right from the start of the experiment. The two spots were paired with different responding legs. Each point represents the mean value from three dogs.

except that of dog 4, for which it was slightly greater than 0.001. The number of sessions required to learn the discrimination showed a mean value of 5.0. After learning was complete the medians of the response times per session showed a mean value of 0.9 second, and the percentage of correct responses per session reached a mean value of 87 per cent. There was no difference between right and left legs in the mean number of sessions required to learn the discrimination, and after learning was complete, there was no significant difference between right and left legs in either response time or percentage of correct responses.

The fourth dog did not behave as did the other three. It showed only a slight improvement in response time during seventeen sessions, but the percentage of correct responses reached a mean value of 81 per cent.

The third type of experiment, performed on three dogs, consisted of training the animals to discriminate between two spots on the body surface by first allowing them to learn well the response to one of the spots and then using the two spots in random order. The spots and legs used were the same as for the previous experiment, and the response to the lumbar stimulus was the one learned first. After this simple one leg response had been learned, it took one or two additional sessions to learn the discrimination. The composite performance curves are shown in figure 1B. After the second spot was introduced, the percentage of correct responses showed a statistically highly significant mean value of 89 per cent (p less than 0.001). There was no significant difference between the performances of right and left legs in either percentage of correct responses or response time.

PROCEDURE AND RESULTS FOR THE HEMIDECORTICATION EXPERIMENTS. The general procedure was that of conditioning dogs to flex a certain limb and then performing a hemidecortication on that side of the cerebrum containing one of the following: (a) the motor cortex of the responding muscles (plus the cortical projection of the u-s where such stimulus was used), (b) the cortical projection of the c-s, (c) both the motor cortex of the responding muscles and the cortical projection of the c-s, (d) neither the motor cortex of the responding muscles nor the cortical projection of the c-s. Six types of experiment were conducted as follows:

I. Two dogs were conditioned in the escape fashion to discriminate between two spots on the left side of the body wall. The particular spots and their respective legs of response were the same as those described above. When this discrimination had been well learned, as shown by the response time and the percentage of correct first movements per session, a left hemidecortication was performed. This should leave the sensory pathways and the cortical projection of the conditioned stimuli intact so that electrical stimulation of either of the spots on the body wall would result in a normal sensation. Further, the motor cortex and the motor pathways of the left foreleg were also left intact. The motor cortex of the right foreleg, however, was completely removed by the operation. (The experiment was performed in this way so that, whatever happened to the response of the right leg as a result of the operation, there would still be the normal left leg with which to compare it.) Three weeks after the operation, the dogs were placed again in the harness and the conditioned responses tested. The operation produced no observable effects on the performance of the animals. The response time and the percentage of correct first movements for either leg showed no change over that previous to the operation.

II. In this experiment, one dog was conditioned in the non-avoidance fashion to flex its right hind leg to the sound of a buzzer and its left hind leg to the sound of a bell. Electrical stimulation of the paw by means of an attached electrode was the u-s and, according to the non-avoidance procedure, was automatically applied on every trial irrespective of the response. The dog was trained to such an extent that when the two conditioned stimuli were administered in random order, the percentage of correct responses per session fluctuated between 90 and 100 per cent.

A left hemidecortication was performed, and three weeks later the performance of the right leg had dropped off to 0 per cent, whereas the performance of the left leg remained unchanged. That the dog might not have been able to hear the c-s was ruled out by several lines of evidence, one of which is sufficient, namely, in response to the c-s for the right leg, the animal would lift the left paw very frequently during the first session after the operation, showing that the buzzer was actually being heard.

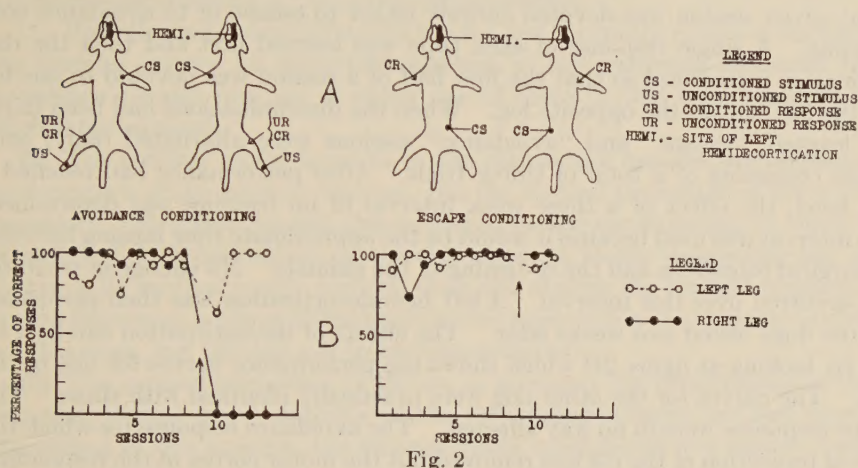


Fig. 2A. Diagram showing from ventral aspect the site of application of the various stimuli, the corresponding legs of response, and the site of the hemidecortication performed after the conditioning was completed. All four combinations shown were carried out on the same animal.

Fig. 2B. Performance curves showing the effect of left hemidecortication on the avoidance and escape responses indicated in figure 2A. The hemidecortication was performed at the arrow.

III. In this experiment, a non-avoidance c-r and an escape c-r were developed in the same leg of one dog. The right foreleg was used, the non-avoidance c-s was a loudspeaker hum, and the escape c-s was electrical stimulation of the left side of the body in the lumbar region. The u-s for the non-avoidance conditioning was electrical stimulation of the paw. In a given session only one type of conditioning was conducted, and the two types of conditioning were alternated in successive sessions.

A left hemidecortication was performed and the responses tested three weeks after the operation. The performance of the non-avoidance c-r had dropped off to 0 per cent whereas the escape c-r remained unchanged.

IV. Two avoidance responses and two escape responses were conditioned in each of two dogs. The c-s for the avoidance training was a punctate pressure stimulus applied to the proximal portion of a foreleg. The c-s for the escape conditioning was the usual punctate electrical stimulus described earlier. The u-s for the avoidance conditioning was electrical stimulation of a paw. The spots of application of the conditioned stimuli and their corresponding legs of response were so chosen (see fig. 2A) that a single hemidecortication would remove (1)

the cortical projection of the c-s for one of the "avoidance" legs (leaving the motor cortex of the responding muscles intact), (2) the cortical projection of the c-s for one of the "escape" legs (leaving the motor cortex of the responding muscles intact), (3) the motor cortex of the responding muscles plus the cortical projection of the *unconditioned* stimulus for the other "avoidance" leg (leaving the cortical projection of the c-s intact), (4) the motor cortex of the responding muscles of the other "escape" leg (leaving the cortical projection of the c-s intact).

Any given session was devoted entirely either to escape or to avoidance conditioning. A single response of each type was learned first and then the discrimination introduced so that the first half of a session was devoted to one leg and the last half to the opposite leg. When the discriminations had been fairly well learned, "escape" and "avoidance" sessions were alternated daily, each session consisting of a total of thirty trials. After performance had reached a high level, the effect of a three week interval of no training was determined. This interval was used because it would be the approximate time lapsing between the surgical procedure and the re-testing of the animals. No change in performance occurred over this interval. A left hemidecortication was then performed and the dogs tested two weeks later. The effects of the extirpation can best be seen by looking at figure 2B which shows the performance curves for one of the dogs. The curves for the other dog were practically identical with these. The escape responses were in no way affected. The avoidance response for which the cortical projection of the c-s was removed but the motor cortex of the responding muscles left intact, showed only a slight impairment of performance. This impairment disappeared by the second postoperative session. The avoidance response for which the hemidecortication removed the cortical projection of the u-s and the motor cortex of the responding muscles, showed complete absence of performance after the operation. The animals would frequently lift the opposite leg instead.

V. Since in the above experiments it was found that a hemidecortication removing either the cortical projection of the c-s or the motor cortex of the responding muscles of escape conditioning did not alter the animal's performance, it was decided to test the effect of a hemidecortication which removed both of these elements. One dog was escape-conditioned in such a way that a c-s applied to the left side of the body wall would elicit flexion of the left foreleg. A right hemidecortication was then performed. The performance was in no way affected.

VI. In this experiment a dog was used that had been conditioned in the escape fashion to flex its right foreleg to a stimulus applied to the left side of the body wall. A previous left hemidecortication (thus removing the motor cortex of the responding muscles) had had no effect upon performance. The plan of this experiment was to determine whether or not the motor cortex of the remaining hemisphere might contain the motor neurons involved in elicitation of the response. The sensori-motor cortex (sigmoid gyrus) of the right hemisphere was therefore removed. The animal's performance was entirely unaltered.

DISCUSSION. The retention of the avoidance response after a hemidecortication which removed the cortical projection of the c-s, leaving the motor cortex of the responding muscles intact, indicates that the cortical projection of the c-s is not a necessary part of the pathways activated by the c-s.

The abolition of the avoidance response by a hemidecortication removing at the same time the cortical projection of the u-s and the motor cortex of the responding muscles, suggests three possibilities for mechanisms involved in avoidance conditioning in the normal intact animal:

(1) Both the cortical projection of the u-s and the motor cortex of the responding muscles occupy an important position in the pathways activated by the avoidance c-s and removal of either one of these (if this were possible) would abolish the response.

(2) The cortical motor neurons of the responding muscles are necessary for performance of the learned response, but the cortical projection of the u-s is not necessary. Evidence against this is that in escape conditioning, in which there is no u-s, hemidecortication on the side opposite to the responding leg (which destroys its cortical motor control) does not abolish the learned response. Of course there may be some difference in motor innervation in avoidance and escape conditioning, but this has yet to be demonstrated.

(3) The cortical projection of the u-s is necessary for performance of the c-r, but the cortical motor neurons of the responding muscles are not necessary. According to this concept, the thing actually conditioned is a sensory image or even a hallucination of the u-s (in this case electrical stimulation of the paw). A neural pathway from the cortical sensory area of the c-s to the sensory area of the u-s is opened by the training procedure. The animal not only experiences the sensation of an electrical stimulus but in addition it experiences it as coming from a particular spot on the body surface. That the ability to localize sensations is a function of the cerebral cortex is well established. By pathways, then, starting at the cortical locus of this sensation the animal lifts the appropriate paw. That a hemidecorticate dog has difficulty localizing sensations on the contralateral body surface is strongly suggested by observations on the dog's behavior when it is pricked with a pin. The animal feels the prick but shows no evidence of an awareness of the site of stimulation as compared to its performance when the normal side of the body is stimulated. Further, according to the present explanation, the c-s after hemidecortication may still be able to elicit the sensory image or the hallucination of the electrical stimulus (at subcortical levels or by cortical elements in the remaining hemisphere), but the animal is unable to localize its source. The impulses giving rise to the conditioned sensation are somehow able to spread to the cortical sensory area of the leg opposite to the correct leg, where there is still good localization, with the resultant flexion of the incorrect leg.

Although all three of these are possibilities, it seems on the basis of the available evidence and the law of parsimony, that the third one is the preferable hypothesis for the time being. The experiments performed on non-avoidance conditioning

indicate that the pathways involved in non-avoidance conditioning are similar to those for avoidance conditioning.

Supporting evidence for these conclusions is found in the experiments of Lang and Olmsted (1923) and of Martino (1939). Lang and Olmsted conditioned hind-leg flexion to a sound, electrical stimulation of the paw being the u-s. Contralateral hemisection of the spinal cord, thus cutting the afferent pathways of the u-s abolished the c-r. Martino found that anesthetization of the site of application of the u-s for eyelid closure abolished the previously acquired c-r. These results are explainable in terms of the hypothesis formulated above. In order for the c-s to elicit a sensory image or an hallucination of the u-s a certain central excitatory state must be maintained at the sensory projection of that u-s. This excitatory state is maintained by a continuous volley of impulses originating in the receptor organs of the u-s, but its magnitude is insufficient to reach the threshold of consciousness.

In escape conditioning, however, the pathways opened must lead from the sensory area of the c-s to the motor area of the responding muscles, there being little likelihood of involvement of another sensory area since there is no u-s.

The retention of the escape responses after all of the extirpations indicates that the cortical motor neurons of the responding muscles are not an essential part of the neural pathways activated by the c-s; nor is the cortical projection of the c-s or the sigmoid gyrus (sensori-motor cortex) of the remaining hemisphere in a hemidecorticate dog. This leaves two possibilities for mechanisms involved in escape conditioning in the normal intact animal:

(a) The neural pathways opened by the training procedure may be so widely distributed in the cerebral cortex that hemidecortication plus removal of the sigmoid gyrus (sensori-motor cortex) of the remaining hemisphere leaves enough of the pathways to permit elicitation of the response by the c-s.

(b) Subcortical pathways in addition to cortical pathways may be opened by the training procedure so that after the various cortical extirpations, the c-s is still able to elicit the response by subcortical pathways. It is well established that the thalamus is a primitive sensory area and the globus pallidus a primitive motor area. Crucial evidence in favor of the opening of pathways at subcortical levels would be the *retention* of an escape response after complete decortication. However, in such an animal, it is very probable that the sham rage phenomenon would completely mask any discrete flexion response that might still be present. Because of this and because all attempts to *develop* discrete conditioned responses in completely decorticate dogs have been without success, the first of the two possibilities mentioned above seems preferable in the present state of our knowledge.

In conclusion it may be pointed out that the fundamental difference between avoidance and escape conditioning is that the principle of substitution (in the usual sense of the term) operates in the former but not in the latter. Where no substitution is involved, neither the cortical projection of the c-s nor the cortical representation of the c-r is required for the retention of a discrete acquired movement. In avoidance conditioning, however, where a third element is

involved, namely, the u-s (for which the c-s is made a substitute) destruction of the cortical representation of this third element abolishes the acquired movement. It appears then that this cortical projection of the u-s is essential for the retention of conditioning which involves the principle of substitution.

SUMMARY

1. A method is described for carrying out escape conditioning in dogs. The conditioned stimulus was applied to a spot on the body surface and the correct response consisted of the discrete flexion of a single leg, thus making possible extirpation of particular portions of sensory and motor projection pathways. The measures of learning were (1) the time interval between the start of the current and the performance of the correct response, and (2) the percentage of correct first movements per session. A single escape response was learned quickly. A discrimination between two spots on the body surface, such that stimulation of one spot elicited flexion of one foreleg and stimulation of the other spot elicited flexion of the other foreleg, could also be learned, but it took somewhat longer than the single response.

2. The effects of hemidecortication on previously conditioned escape and avoidance flexion responses were observed. Under controlled conditions it was shown that a hemidecortication that removed (1) the cortical projection of the conditioned stimulus leaving the motor cortex of the responding muscles intact did not interfere with performance in either escape conditioning or avoidance conditioning; (2) the motor cortex of the responding muscles (leaving the cortical projection of the conditioned stimulus intact) likewise did not interfere with performance in escape conditioning; (3) the motor cortex of an avoidance response plus the cortical projection of the *unconditioned* stimulus (leaving the cortical projection of the conditioned stimulus intact) completely abolished the response.

Further, a hemidecortication for escape conditioning which destroyed both the cortical projection of the conditioned stimulus and the motor cortex of the responding muscles did not interfere with performance.

A surgical procedure that included (a) a hemidecortication removing the motor cortex of the responding muscles, and (b) extirpation of the sensori-motor cortex (sigmoid gyrus) of the remaining hemisphere did not interfere with performance of an escape conditioned response.

3. It was concluded that in avoidance conditioning, the cortical projection of the unconditioned stimulus occupies an important position in the neural pathways activated by the conditioned stimulus in the normal intact animal. The conditioned stimulus possibly becomes able to elicit a sensory image or even a hallucination of electrical stimulation of a particular paw.

It was also concluded that in escape conditioning there is no localized cortical structure necessary for elicitation of the acquired response. Either the neural pathways involved are widely distributed throughout the cerebral cortex or pathways are opened at subcortical levels by the training procedure. The pathways opened must lead from a sensory area of the conditioned stimulus to a motor area of the responding muscles, there being little possibility of involvement of another sensory area since there is no unconditioned stimulus.

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